[Communicative & Integrative Biology 1:2, 146-147; October/November/December 2008]; ©2008 Landes Bioscience

Article Addendum

Habitat loss, dispersal, and the probability of extinction of tree species

Daniel Montoya

Departamento de Ecología; Universidad de Alcalá; Madrid Spain

Key words: dispersal, trees, habitat loss, extinction, animal, wind

Ecological studies show that species not equally decline following habitat destruction, and suggest that underlying biological processes, such as dispersal type, might be determining the ecological sensitivity of species to habitat loss. There is, however, uncertainty as to how these mechanisms scale up to large scales and generalize across ecosystem types and processes, especially in plants. Using data from ~90,000 forest survey plots covering Peninsular Spain, we explored the patterns of variation in the probability of occurrence of 34 common tree species to decreasing levels of local forest cover. Decreased forest cover had a strong negative effect on tree diversity, but the responses of individual species were highly variable. Interestingly, animal-dispersed species were less vulnerable to habitat loss than wind-dispersed species. However, the latter is true provided that animal dispersers persist in the forest system. These results highlight the importance of plant-animal interactions in preventing the collapse of forest communities under habitat destruction.

Habitat destruction is the leading cause of the global biodiversity loss in the world. According to the FAO, deforestation produced an annual average loss of 12 million hectares between 1980 and 1995,[1] and has physically changed forest landscapes in all continents. These changes alter the physical space where species grow and interact, and thus trigger biological responses that may lead to biotic collapse. There is evidence however that not all species equally decline towards extinction following habitat destruction, with some species being at greater risk in fragmented landscapes than others.[2,3] Therefore, a major conservation task for ecologists consists on identifying the factors that globally drive species sensitivity to habitat loss.

Recent studies on spatially structured populations have highlighted the potential importance of dispersal in allowing the persistence of forest species in fragmented landscapes.[4,5] For plants, dispersal patterns largely depend on their dispersal agents. Dispersal by wind is likely much closer to random than dispersal by animals due to animals actively deliver seeds toward suitable patches (directed dispersal). Moreover, some forms of animal dispersal increase the average dispersal distance.[6] Both directed dispersal and long dispersal distances would help keep physically isolated habitat patches demographically connected from a tree's point of view (Fig. 1). These observations, rooted in the metapopulation theory,[7] suggest that the direct effects of habitat loss are likely to be less pronounced for animal-dispersed species than they are for wind-dispersed species. To test this hypothesis, we analyzed the relationship between local forest cover and the occurrence of 34 canopy dominant tree species (28 native to the study region and six exotic) in 89365 different survey sites (approximate density of one plot per 1 Km^2) distributed across peninsular Spain (492,173 Km^2).

According to previous studies in this topic,[8] habitat destruction reduced overall species richness in the study region. However, we found a significant interspecific variation in the individual responses to habitat loss, indicating that tree species responded differently to the effects of forest loss. A significant portion of this variation could be explained by the primary seed dispersal mode, with species having morphological adaptations for dispersal by animals less vulnerable than species morphologically-adapted for wind dispersal. To evaluate the robustness of these results we examined various competing explanations that might be behind the observed pattern, such as those emerging from the contrasted phylogenetic composition among tree species, the climate heterogeneity in the study region (the so-called multicollinearity problem), soil, major perturbation events (e.g., fire), and random effects. The results were robust regardless of these alternative hypotheses: although significant unexplained variation remained in the response of species within each dispersal group, we found that animal-dispersed species are, on average, less vulnerable to decreased forest cover than wind-dispersed species.

The implications of these results are obvious: deforestation is more likely to threaten a given wind-dispersed, than a given animal-dispersed, plant species. However, this prediction must take into account the within-group variation in the response to deforestation, and the degree of persistence of animal dispersers that also face the negative effects of habitat loss. The latter is crucial given that, in the absence of dispersal vectors, animal-dispersed trees would not be able to disperse their seeds away from the parent tree. This process would affect severely the reproductive rates of tree species and might eventually drive trees to extinction. Both computer simulations and empirical studies focusing on the relationship between habitat loss and animal persistence have shown that higher trophic groups are

Correspondence to: Daniel Montoya Terán; Departamento de Ecología; Universidad de Alcalá; Edificio de Ciencias; Campus Universitario; 28871 Alcalá de Henares; Madrid, Spain; Tel.: +918856406; Fax: +918854929; Email: daniel.montoya@alu.uah.es

Submitted: 09/16/08; Accepted: 09/17/08

Previously published online as a *Communicative & Integrative Biology* E-publication: http://www.landesbioscience.com/journals/cib/article/6998

Addendum to: Montoya D, Zavala MA, Rodríguez MA, Purves DW. Animal versus wind dispersal and the robustness of tree species to deforestation. Science 2008; 320:1502–4; PMID: 18535208; DOI: 10.1126/science.1158404.

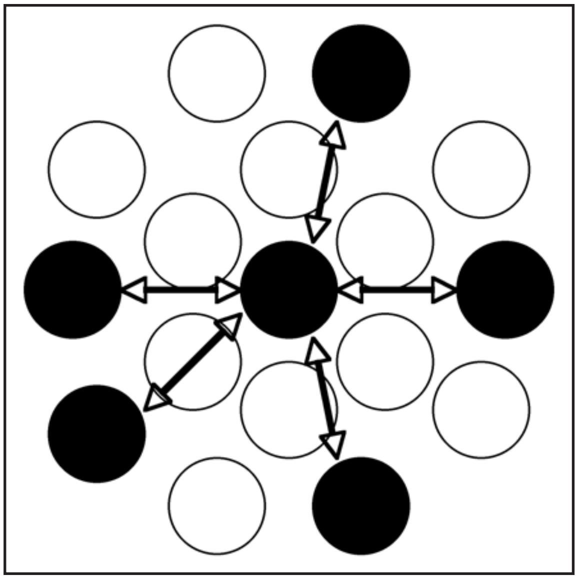

Figure 1. Simulation of a fragmented landscape: white circles represent areas where forest has been lost; black circles correspond to remnant forest patches. Landscape connectivity from a tree's perspective partially depends on the tree's dispersal mode. For an animal-dispersed tree, directed dispersal and long dispersal distances would help keep physically isolated habitat patches demographically connected, which is represented by the arrows.

more prone to extinction under habitat loss than primary producers.[9] Moreover, there is evidence for a positive correlation between body size and vulnerability to extinction.[10] Because body size differences among animal dispersers seem to affect dispersal distances of trees, with large animals transporting seeds to longer distances than small ones,[11,12] it can be hypothesized that habitat loss will likely decrease progressively the average dispersal distances of animal-dispersed tree species due to the extinction of the big dispersers. With no account of occasional long dispersal events,[13] the higher vulnerability of animals to habitat loss might disrupt the dispersal process of zoochorus tree species, in a similar way to the recently reported crisis in pollination networks.[14]

The picture given above might be even more dramatic if we take into account the potential interactions between habitat loss and global change. Although the history of life has suffered from several climate changes in the past, the current process differs in their faster rates of change compared to previous episodes.[15] This, coupled with a significant reduction of suitable habitat to biological colonization due to habitat loss, will likely result in the inability of trees species to track changes in climate space. In contrast to more mobile organisms, range shifts for immobile species with long generation times like trees rely entirely on dispersal vectors, so preserving mutualistic networks will be a key factor to guaranty the biodiversity of the future.

Our large-scale approach supports the idea that links among habitat cover and population-level processes such as dispersal can be generalized to large scales and across ecosystem types and processes. This functional approach provides useful information about what traits and species are more sensitive to habitat destruction, likely future shifts in the species composition of forest communities, and clues to address conservation policies. We have demonstrated that, in the context of dispersal, plant-animal interactions not only create and maintain biodiversity,[16] but also increase the degree of resilience of forest systems to perturbations such as habitat loss. However, more studies focusing on biological responses to habitat destruction are needed, with special emphasis on how biodiversity will respond to the effects generated by the interaction between landscape structure and global change.

Acknowledgements

Daniel Montoya was supported by a FPU fellowship from the Spanish MEC (AP2004-0075).

References

1. Food and Agriculture Organization of the United Nations, State of the World's Forests, 1997, FAO, Rome 1997; 16.
2. Tilman D, May RM, Lehman CL, Nowak MA. Habitat destruction and the extinction debt. Nature 1994; 371:65-6.
3. Henle K, Davies KF, Kleyer M, Margules C, Settele J. Predictors of species sensitivity to fragmentation. Biodivers Conserv 2004; 13:207-51.
4. Purves DW, Dushoff J. Directed seed dispersal and metapopulation response to habitat loss and disturbance: application to *Eichhornia paniculata*. J Ecol 2005; 93:658-69.
5. Purves DW, Zavala MA, Ogle K, Prieto F, Rey-Benayas JM. Environmental heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in Mediterranean Spain. Ecol Monogr 2007; 77:77-97.
6. Johst K, Brandl R, Eber S. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. Oikos 2002; 98:263-70.
7. Hanski I. Metapopulation Ecology. Oxford, UK: Oxford Univ Press 1999.
8. Fahrig L. Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Syst 2003; 34:487-515.
9. Solé RV, Montoya JM. Ecological network meltdown from habitat loss and fragmentation. In: Pascual M, Dunne JA, eds. Ecological Networks: Linking Structure to Dynamics in Food Webs. New York: Oxford Univ Press 2006; 305-24.
10. Cardillo M, Bromham L. Body size and risk of extinction in Australian mammals. Conserv Biol 2001; 15:1435-40.
11. Jordano P, García C, Godoy JA, García-Castaño JL. Differential contribution of frugivores to complex seed dispersal patterns. Proc Natl Acad Sci USA 2007; 104:3278-82.
12. Spiegel O, Nathan R. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. Ecol Lett 2007; 10:718-28.
13. Higgins, SI, Nathan R, Cain ML. Are long-distance dispersal events usually caused by nonstandard means of dispersal? Ecology 2003; 84:1945-56.
14. Kearns CA, Inouye DW, Waser NM. Endangered mutualisms: the conservation of plant-pollinator interactions. Annu Rev Ecol Syst 1998; 29:83-112.
15. IPCC (Intergovernmental Panel on Climate Change). Climate Change 2001—The scientific basis. 2001. Cambridge: Cambridge Univ Press.
16. Bascompte J, Jordano P. The structure of plant-animal mutualistic networks: the architecture of biodiversity. Ann Rev Ecol Evol Syst 2007; 38:567-93.